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Construction and structure of the semidomes of the fiddler crab *Minuca rapax* (Brachyura: Ocypodidae) in southern Brazil

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ABSTRACT

Fiddler crabs construct and maintain above-ground sedimentary structures that vary in shape and function. We describe for the first time the behavior of the construction of semidomes, a type of sedimentary structure, in *Minuca rapax* (Smith, 1870) and the relationship of semidomes to other fiddler crab structures. We observed how semidomes are built and explored the relationship between the builders and semidome traits. Males use their first three ambulatory legs to pick up sediment from the surface and deposit sand at the edge of the opening to their burrows, shaping the semidome with their legs, carapace, and large claw. We found a positive relationship between the carapace width (CW) of the resident crab and two semidome measurements: structure width and burrow diameter, but there was no relationship between resident crab CW and semidome height.

Key Words: animal architecture, extended phenotype, hoods, sedimentary structures

Fiddler crabs (Ocypodidae) occur in soft intertidal sediments in tropical through warm temperate regions worldwide (Crane, 1975). Courting males and females build mud or sand structures at the entrance to their burrows (Christy & Wada, 2015). The shapes of these structures and hence their names vary (e.g., semidomes, hoods, pillars, chimneys, and rims) as do their functions: mate attraction (Zucker, 1981; Christy *et al.*, 2001), landmark orientation (Ribeiro *et al.*, 2006), and concealment of burrow entrance (Slatyer *et al.*, 2008). Semidomes are half-domes that consist of semicircular structures projected above the burrow entrance (Fig. 1). At least ten species of fiddler crabs build massive semidomes (Table 1), including *Minuca rapax*, widespread in the Western Atlantic Ocean (Thurman *et al.*, 2013). Overall, semidomes could serve to attract females, as landmark orientation, and to reduce aggressiveness among males (Table 1). Despite experimental and observational studies on the milky fiddler crab *Austruca lactea* (De Haan, 1835) (Kim *et al.*, 2004; Zhu *et al.*, 2012), little is known about other semidome builders. We describe for the first time the semidome building process of *M. rapax*, characterizing the building behavior and relating the structure with the morphology of crabs.

The study was conducted Juréia-Itatins Ecological Station in an estuary at Barra do Una (24°24′50″S, 47°04′14″W), southern coast of Brazil, during March and April/2015. Observations were conducted at spring low tides in a sand/muddy, non-vegetated area. We observed semidome construction by scanning the area for active builders and then watched their behavior for two hours (focal-animal sampling). Building behavior was recorded for 11 individuals with a total of 22 h of observation. We kept a distance of at least 1.5 m, which did not appear to affect the behavior of crabs. We also estimated the density of semidome builders by sampling 1 m^2 plots (N = 10) located randomly in the study area (~150 m^2). We did not remove crabs from their burrows, and after ~15 min, all crabs in each plot resumed normal behavior. The number of active crabs in the plot and the number with complete (Figs. 1A, B, 2) or incomplete semidomes were recorded. Along the study area, 26 burrows of *M. rapax* had their semidomes measured: height (H), width (W), and diameter (BD), as well as the carapace width (CW) in mm of the builder. We used a simple linear regression analysis to assess the relationship between CW and the characteristic of the structures (H, W, and BD).

The density of male and female *M. rapax* was low (3.4 individuals/m^2) and the majority of adult males (1.3 individuals/m^2; 17.65 ± 2.79 mm CW) had burrows with an associated semidomes (54% complete; 29% incomplete and 17% males without semidomes). Only males built semidomes during low tide, as it is true for other species that build semidomes (Kim *et al.*, 2004).

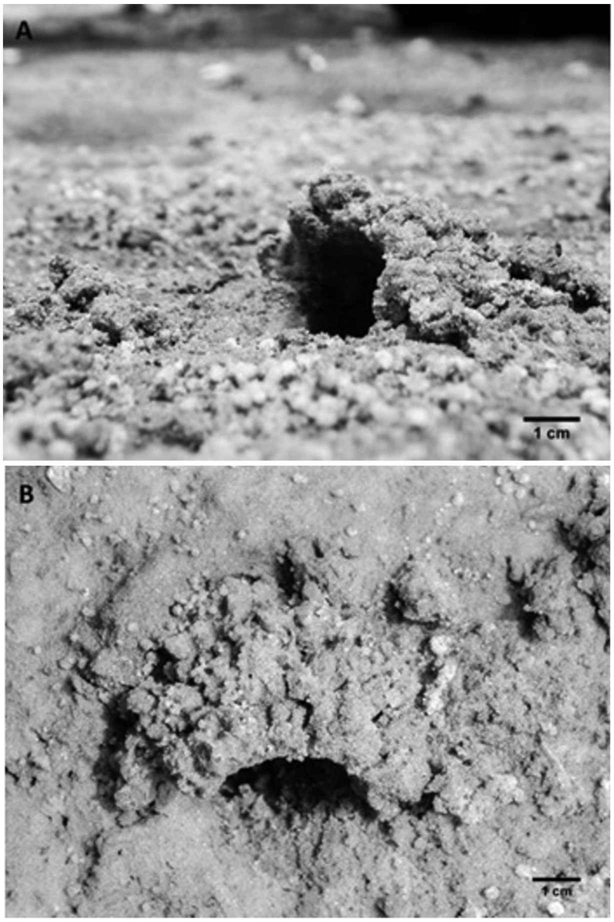

Figure 1. Semidome structure constructed by *Minuca rapax:* side **(A)** and top views **(B)**.

Males used their first, second, and third ambulatory legs to pick up and carry surface sediment from around the entrance to their burrow. They sometimes picked up pellets of sediment they had removed from burrows. Males used the same legs to shape material to form an arched semidome by pushing sediment upward from the inside with the dorsal surface of their carapace as well as with the outer surface of the manus of their large claw. Not all males built semidomes (6 out of 34 individuals). The observed males seemed to invest in activities other than building, such as stealing burrows, investing in courtship display signaling or foraging. The semidome construction described for *M. rapax* was similar to that described the fiddler crabs *L. leptodactyla* Rathbun, 1898 (Matthews, 1930) and *A. lactea* (Kim *et al.*, 2004), but different from that described for *M. pugnax* (Smith, 1870) by Crane (1975), in which males simply pushed up soft sediment from the ceiling of their burrows.

Semidome-building is a condition-dependent behavior carried out by at least ten species of fiddler crabs (Table 1). One such species, *M. cf. virens* Salmon & Atsaides, 1968 had been previously considered as a synonym of *M. rapax* (e.g., Beinlich & von Hagen, 2006) or as a separate species (e.g., Shih *et al.*, 2016). There are no external morphological differences between the two species, which complicates their identifications, only variations in the structures of the gastric mill (Shih *et al.*, 2015). Both species, however, build semidomes and the sedimentary structure should not be used to differentiate *M. cf. virens* and *M. rapax*.

Large males (mean CW ± SD 17.65 ± 2.79 mm) built larger semidomes (width 32.17 ± 7.47 mm) (Fig. 3A). Christy *et al.* (2001) showed similar results for males of *Leptuca terpsichores* Crane, 1941. Burrow diameter (BD) (14.88 ± 2.26mm) was positively correlated to CW (Fig. 3B). Similar relationships were observed in studies for other fiddler crabs (e.g., Kim *et al.* (2004), Lim (2006), Machado *et al.* (2013)), which also suggested a dependence between resident size and BD, and the amount of sediment that crabs carry to build semidomes and, consequently, which will be reflected on the size of semidomes. There was no relationship between the height of semidomes (11.4 ± 3.34 mm) and CW, differing from previous results for semidomes of *A. lactea* (Kim *et al.*, 2004) (Figure 3C). Such negative correlation in *M. rapax* could be explained by the absence of a functional value of higher structures, as observed by Yamaguchi *et al.* (2005) in the poorly-formed hoods of *A. perplexa* (H. Milne Edwards, 1852), which were considered non-functional against intruders or as ornamentation to attract females. Another possibility is that some small males intentionally build higher

Table 1. Summary of semidome structures built by fiddler crabs and their general characteristics; (?), non-tested hypothesis. Taxonomy based on Shih *et al.* (2016).

Species	Sex	Functions	Reference
Austruca annulipes (H. Milne Edwards, 1837)	both sexes	–	Mokhlesi et al.(2011)
Austruca lactea (de Haan, 1835)	male	Landmark orientation, burrow defense, sexual signal	Kim et al. (2004, 2010, 2017), Zhu *et al.* (2012)
Leptuca latimanus Rathbun, 1893	male	Reduction of aggressive behavior, sexual signal	Zucker (1981)
Leptuca pugilator (Bosc, 1802)	male	Burrow defense (?)	Christy (1982)
Leptuca uruguayensis Nobili, 1901	male	–	Ribeiro *et al.* (2016)
Leptuca leptodactyla Rathbun, 1898	male	Burrow defense (?), sexual signal	Matthews (1930), Masunari (2012)
Minuca cf. virens Salmon & Atsaides, 1968	male	–	Powers & Cole (1976)
Minuca minax (LeConte, 1855)	male	Acoustic signal enhancement (?)	Montague (1980)
Minuca pugnax (Smith, 1870)	both sexes	Reduction of combats between neighbors (?), acoustic signal enhancement (?) reduction of erosion by tidal action (?), sexual signal	Crane (1975), Montague (1980), Greenspan (1982)
Minuca rapax (Smith, 1870)	male	–	Present study

structures, as Christy *et al.* (2001) suggested for small males of *L. terpsichores*, which tend to build higher structures to increase their conspicuousness.

Some studies refer to semidomes as a type of hood that serve to attract females (e.g., Greenspan, 1982; Zhu *et al.*, 2012). These structures mimic natural objects and females tend to approach them, which in turn may reduce predation risk (Christy *et al.*, 2003). Because our study was carried out at the end of the reproductive season, we did not observe female approaches, which could have affected semidome height in the field (Christy *et al.*, 2001; Kim *et al.*, 2004). The semidomes of *A. lactea* could act as sexual signals to attract females (Kim *et al.*, 2004; Yamaguchi *et al.*, 2005; Zhu *et al.*, 2012). Zhu *et al.* (2012) showed a link between the size of male-built structures and female choice, indicating a preference for larger semidomes. Zucker (1981) observed that *U. latimanus* semidomes act as a courtship signal and are also linked to high density, which in turn is related to aggressive behavior, reducing combat between neighboring crabs. Further detailed studies are required to identify the function of semidome construction in *M. rapax* and other fiddler crabs.

Figure 2. Male *Minuca rapax* and semidome structure.

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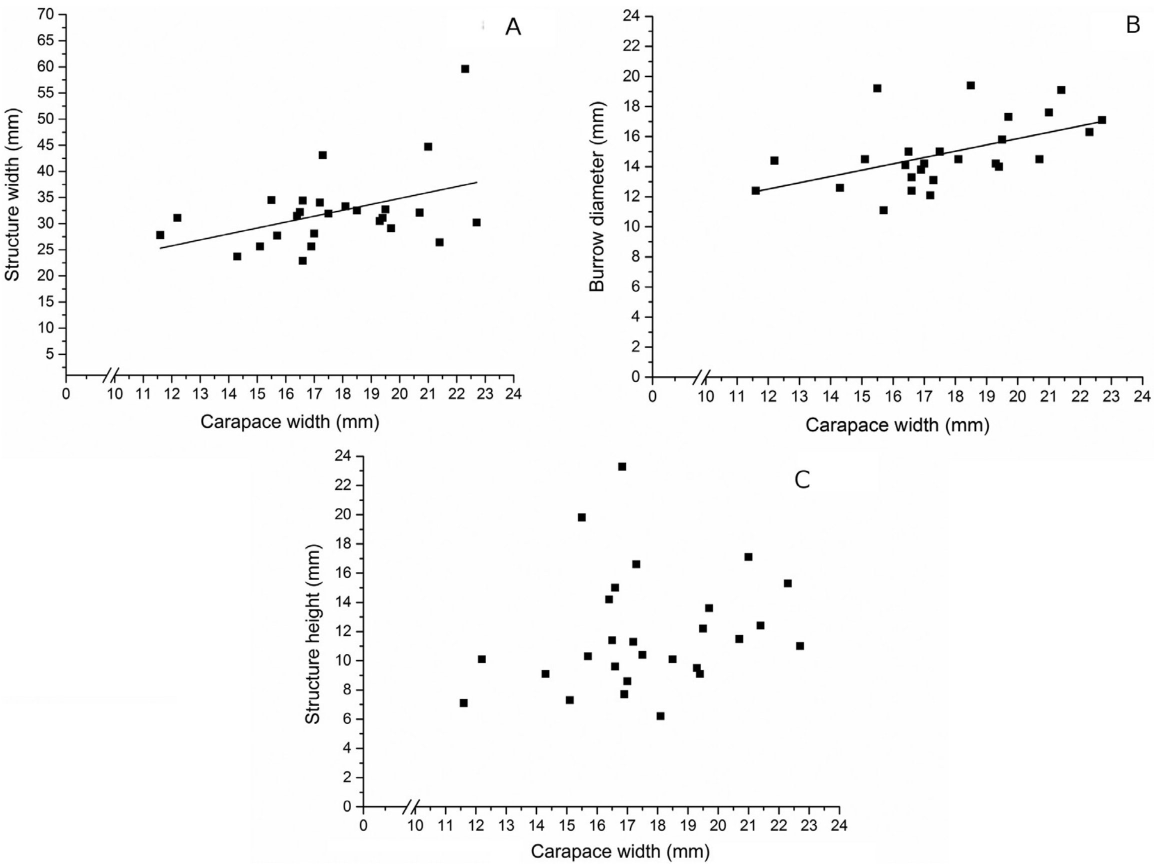

Figure 3. Simple linear regression analysis. Positive relationship between carapace width (CW) of *Minuca rapax* and semidome width (W) (regression: $N = 26$, $df = 25$, F = 5.24, $r^2 = 0.179$, $P = 0.03$) (**A**); Positive relationship between CW and burrow diameter (BD) (regression: $N = 26$, $df = 25$, F = 8.85, $r^2 = 0.270$, $P = 0.006$) (**B**); no relationship between CW and structure height (H) (regression: $N = 26$, $df = 25$, F = 2.19, $r^2 = 0.84$, P = 0.1515) (**C**).

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